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# Research report

# Binding Body andSelf in Visuo-Vestibular Conflicts

Gianluca Macauda[1], Giovanni Bertolini[1], Antonella Palla[1],Dominik Straumann[1,2], Peter Brugger[1,2], Bigna Lenggenhager[1,2]

[1]Department of Neurology, University Hospital Zurich,Switzerland

[2]Zurich Center for Integrative Human Physiology, University of Zurich, Switzerland

Correspondence to:
BignaLenggenhager
Neuropsychology
Department of Neurology
University Hospital Zurich
Frauenklinikstrasse 26
CH-8091 Zurich, Switzerland
phone: +41 44 255 55 84
email: bigna.lenggenhager@gmail.com

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## ABSTRACT

Maintenance of the bodily self relies on the accurate integration of multisensory inputs wherebyvisuo-vestibular cue integration is thought to play an essential role. Here, we tested in healthy volunteers how conflicting visuo-vestibular bodily input might impact on body-self coherence in a full body illusion set-up. Natural passive vestibular stimulation was provided on a motion platform, while visual input was manipulated using virtual reality equipment.Explicit (questionnaire) and implicit (skin temperature) measures were employed to assessillusoryself-identification with either a mannequin or a control object. Questionnaire results pointed to a relatively small illusion,but thehand skin temperature, plausibly an index of illusory body ownership,showed the predicted drop specificallyin the condition when participants saw the mannequin moving in **congruence** with them. We argue that this implicit measure was accessible to visuo-vestibular modulation of the sense of self, possibly mediated by shared neural processes in the insula involved in vestibular and interoceptive signaling, thermoregulation and multisensory integration.

## 1. INTRODUCTION

Thesense ofthe"self" and its relation to the body has always fascinatedmankind and has increasingly been studied in empirical research. Recent models suggest that the self is grounded in neural mechanisms representing the body, andthus cruciallyrelies on successfulmultisensory integration(for a review see Blanke, 2012). Failure of such integration results in disturbances of the bodily self, apparent in various neurological and psychiatric conditions(e.g. somatoparaphrenia and autoscopic phenomena, see Brugger & Lenggenhager, 2014 for a recent review).Experimental evidence further-shows that the bodily self can be manipulatedin systematic and predictable ways by introducing a conflict between two or more sense modalities. During spatially conflicting body-related information, one sensory system (e.g. vision) dominates the information from other sensory modalities (e.g. proprioception or touch). This might result in an illusory ownership fora body part, e.g. a seen fakehand(Botvinick & Cohen, 1998), foot (Lenggenhager *et al.*, 2014), face(Tsakiris, 2008; Sforza *et al.*, 2010)oreven a full body(Lenggenhager *et al.*, 2007; Petkova & Ehrsson, 2008).These illusionshave been linked tospecific properties of multimodal neurons(e.g. Graziano & Botvinick, 2002)andinvolve a networkof premotor, temporo-parietal and insular areas(for recent reviews see Lenggenhager & Lopez, in press; Blanke, 2012).

Theconflicts inducing body part and full body illusions (FBI) initially involved the visual and tactile modalities. Specifically, felt touch on an unseen body part in synchrony with visually observed touch on a corresponding artificial body part led to an illusory feeling of ownership for the latter (Botvinick & Cohen, 1998). **Recentpublicationshaveemployed**conflicts between other modalitieswere alsoemployed,e.g. between visual and sensorimotor(Tsakiris *et al.*, 2006; Kannape *et al.*, 2010), visual and nociceptive (Capelari *et al.*, 2009), visual and cardiac(Aspell *et al.*, 2013; Suzuki *et al.*, 2013), visual and respiratory (Adler *et al.*, 2014), visual and proprioceptive (Walsh *et al.*, 2011),proprioceptive and tactile(Ehrsson *et al.*, 2005) or auditory and tactile(Senna *et al.*, 2014)information.

No study so far has tried to induce bodily illusions by manipulating the information deriving from concurrent stimulation of the visual and vestibular senses. This is surprising, as an increasing number of clinical observations have suggested a critical role of visuo-vestibular integration for binding body and self(e.g. Devinsky *et al.*, 1989; Blanke *et al.*, 2002, 2004; Blanke, 2004; Brandt *et al.*, 2005; De Ridder *et al.*, 2007; Ionta *et al.*, 2011; Mazzola *et al.*, 2014). Likewise,experimental findingspoint to a crucial contribution of the vestibular system to the bodily self (for recent reviews see e.g.Lenggenhager & Lopez, in press; Lenggenhager *et al.*, 2006; Lopez *et al.*, 2008; Blanke, 2012; Lopez, 2013; Pfeiffer *et al.*, 2014).For the latter, mental simulation of changes in self-location and disembodiment (i.e. own-body transformation) can be markedly altered during vestibular stimulation (Lenggenhager *et al.*, 2008; Falconer & Mast, 2012; van Elk & Blanke, 2014), and importantly, this applies only to full bodies but not to body parts (Falconer & Mast 2012).Accordingly, functional imaging studies during full body illusions associated illusory changes in first-person perspective and self-location with altered activity and connectivity in the bilateraltemporo-parietal junction, a multisensory area which is part of the so-called “vestibular cortex” network (Ionta et al., 2011, 2014).

Visuo-vestibular cue integration is essential for self-motion, motor control, and spatial orientation and hencefor the interaction with our environment(for a review see Fetsch *et al.*, 2010) and the demarcation of self from non-self(Lopez, 2013).Visuo-vestibular cues are normally merged in a statistically optimal fashion, with vision helping to discriminate ambiguous vestibular signals,and also vice versa(**MacNeilage*et al.*,**

**2007; Fetsch*et al.*, 2009; Berger *et al.*, 2010; Butler *et al.*, 2010, 2014; Prsa*et al.*, 2012**).

In view of the strong link between the vestibular system and aspects of the bodily self, we set out to fill the gap in current research using multisensory illusions by testing visuo-vestibular cue integration in a FBI setup. Following the paradigm of previous FBI studies (Petkova & Ehrsson, 2008), participants observedeither a body (mannequin) or an object moving with respect to the groundfrom first-person perspective through a head mounted display (HMD).This approachcomplements traditional studies investigating visuo-vestibular cue integration using more general optic flow (MacNeilage *et al.*, 2007; Fetsch *et al.*, 2009; Berger *et al.*, 2010; Butler *et al.*, 2010; Prsa *et al.*, 2012) and allows to link it more directly to the concept of the bodily self.**Congruence** between visual and vestibular information was manipulated by altering visual input during passive whole-body movements. Explicit changes in the bodily self were assessed by a questionnaire,while skin temperature was recorded as an implicit measure;previous studies have shown a drop in skin temperature during illusory self-identification with a fake hand (Moseley *et al.*, 2008; Hohwy & Paton, 2010; Kammers *et al.*, 2011; Tsakiris *et al.*, 2011)oran artificial body(Salomon *et al.*, 2013). In accordance with these findingswe expecteda stronger FBI during visuo-vestibular **congruent**stimulation of the own body and that of a mannequin. We also predicted an accompanying drop in skin temperature.

## 2. METHODS

### 2.1 Participants

Twenty-one healthy volunteers participated in the experiment (13 female, mean age = 25.9±1.33, 17 right handed). All participants had normal or corrected to normal vision, were fluent in German,reported no history of motion sickness nor of any neurological or psychiatric disorder. The study was approved by the local Ethics Committee and conducted according to the ethical standards of the Declaration of Helsinki. All participants gave written informed consent before the experiment. At the end, participants were debriefed and received a remuneration of 20 Swiss francs.

## 2.2 Procedure

### 2.2.1 General procedure

Participants were comfortably seated on a motion platform. Their head was fixed at the back of the seat with a head-shaped pillow and from the sides with two adjustable hard fixation pillows.They were encouraged to relax and not to move during the experiment.Earplugs and white noise presented throughheadphones were used to cancel out the noise of the motion platform. Participants wore a HMDfor the video presentation (see2.2.2 Experimental Setup) and were required to keep their hands in the grasping posture around a horizontal pole in front of them, as taken at the begin of the experiment. Thermo-sensors(see 2.3.2 Temperature) were attached to the participants' hands and neck.

The experiment consisted of four conditions presented in a counterbalanced order. Each condition lasted about two minutes and was followed by a questionnaire displayed on theHMD. After the experiment, participants underwent asemi-structured interviewaskingabout their experiences and thoughts while being seated on the motion platform.

### 2.2.2 Experimental Setup

The experiment was conducted on a motion platform with six degrees of freedom (E-Cue 624-1800 motion system, FCS Simulator Systems, Schiphol, Netherlands). The platform delivered a sequence of translationalaccelerations (ranging from 0.16 $m/s^2$to 0.9 $m/s^2$) along the earth-horizontal interaural axislasting between 3 and 12 s for an overall stimulus duration of 120 s (see Figure 1E/F for the exact motion pattern). This movement pattern, identical for all the **participants** and conditions, was selected in order to provide a passive vestibular stimulation that wasclearlydetectable but not nauseating. Capitalizing on results from the rubber hand illusion (RHI),suggesting a stronger illusion when stroking was applied irregularly(Petkova & Ehrsson, 2009), different accelerations and amplitudes (distances) wereused within themotion pattern.

The seat for the participants was positioned in the center of the platform (Figure 2). A life-size mannequin dressed in white and with realistically looking rubber hands (Figure 1A/B)or a red roundish object of about the same size (Figure 1C/D) was positioned on the posterior part of the platform facing thedirection opposite to that of the participant.

EXpyVR (http://lnco.epfl.ch/, expyvr) was used for video and questionnaire presentation, and for recording the responses. The movements were filmed with a Logitech c930e webcam(Logitech, Lausanne, Switzerland) with a maximal width of 640 pixels. The video feed was sent to a laptop connected to the HMD(Oculus Rift, Oculus VR, Irvine, USA). The head tracking system implemented in the Oculus Rift was disabled. The video was displayed with a resolution of 1280 x 768 pixelsand an approximately90° field of view in the horizontal plane.Participants responded to the questionnaire with their right hand using a joystick (Competition Pro USB, Speedlink, Weertzen, Germany) mounted in front of them.

### 2.2.3 Visual Stimuli

Visual stimuli consisted of video clips presented for the entire movement duration. The camera that recorded the movies from aspace-fixed position on the motion platform, recording either the mannequin or a red pillow (object) from above (i.e. a first person perspective - see Figure 1 A-D). In the ***congruent***conditions, participants saw the mannequin or the object in real time and left-rightmirrored by the presentation software. In this way, the seen movement corresponded to the felt movement. In the ***incongruent*** conditions, a temporal delay of one second was introduced by the softwareandadditionally the video was not mirrored, thus, creating a temporal and spatial incongruence at the same time. In this way the participants saw the movement temporally delayed and in the direction opposite to how they experienced it.This ***incongruent*** condition was chosen based on pretests in order to increase the conflict between visual and vestibular cues.

### 2.3 Measurements of the illusion

#### 2.3.1 Questionnaire

A questionnaire modified after Lenggenhager et al.(2007) and Petkova&Ehrsson(2008)was used in a German version to assess subjective aspects of the visuo-vestibular illusion (see Table 1for an English translation of all items). Subjective ratings were recorded with a 30-steps visual analog scale using a joystick in which the left-most positionrepresented“very weak” and the right-most position “very strong”The order of the questions was randomized over conditions and participants. An illusion score was calculated from the average of questions Q1, Q2 and Q4. Q2 was developed as an illusion question during pretests, as some participants spontaneouslyremarked the sensation of the feet floating in the air in the **congruent** mannequin condition despite the fact that the feet touched the platform. As in the seen video the mannequin and the object were floating, we thought that this question would be an interesting measure of visual capture of proprioception/touch and thus self-identification. In the traditional RHI literature, Q3 is usually considered a control question ("having two left/right hands"). However, in the present context of a vestibular induced FBI we do not consider it as a pure control question and thus report it separately. This decision was based on both clinical observations of multiple bodily consciousness (Brugger *et al.*, 2006) and corresponding experimental findings (Heydrich et al., 2013) and further reinforced by pilot experimentation. Q5 assessed the perceived match between the seen and the felt movement, while Q6 provided a measure for the perceived sickness during vestibular stimulation.

### 2.3.2 Temperature

Skin temperature was measured with a HH309A Data Logger Thermometer (Omega, Stamford, USA) following the procedure of Salomon *et al.*(2013). Two of the four thermocouples were placed on the dorsal part of the left and right hand, while one thermocouple was attached to the left side of the neck (over the sternocleidomastoid muscle). The fourth thermocouple was used to control room temperature and attached to the seat (see supplementary online material). Temperature was measured with a sampling rate of 0.5 Hz during each condition for the entire length of visuo-vestibular stimulation beginning six seconds before stimulation forestablishing a baseline.

## 2.4Data preprocessing and analysis

### 2.4.1 Data preprocessing

In one participant the temperature recording stopped due to technical issues and he was thus excluded from the temperature analysis. In another participant, the thermocouple attached to the neck fell off,therefore only hand temperature was included in the analysis.

In a first step, a temperature baseline was calculated for each participant by averaging three data points taken from the period of six seconds before movement initiation. To compute temperature changes over time,we calculatedfor each condition four periodsfrom the 58 data points, averaging14 (mean t1 and t2) or 15 (mean t3 and t4) datapoints respectively. T1 thus corresponded approximately to the first 30seconds of stimulation, t2 to seconds 30 to 60, t3 to seconds 60 to 90, and t4 to seconds 90 to 120.Moreover, temperature data from the left and right hands were averaged.Temperature changes were calculated by subtracting the baseline from the four averaged temperature data points (t1 to t4). To differentiate between illusion-induced temperature changes and unspecific changes over time, we subtractedfor each averaged data point (t1 to t4)the mean over all four conditions(***congruen****t mannequin,* ***incongruent*** *mannequin,* ***congruent*** *object,* ***incongruent*** *object*)for that time point separately for the hand and the neck data.

### 2.4.2Statistical analysis

Statistical analysis was performed using IBM SPSS Statistics 21 (IBM Corp., Armonk, NY, USA).

*Questionnaires*

For the questionnaire data threeseparate 2 × 2 repeated measuresANOVAs with within subject factors *body*(mannequin, object) and *congruence*(**congruent, incongruent**) were calculated for the illusion score (mean Q1, Q2, and Q4), for Q5, Q6, and for Q3. For these analyses, data from all 21 participants were used.

*Skin temperature*

To assess changes in skin temperature, a2 × 2 × 4 × 2 repeated measuresANOVA with factors *body* (mannequin, object), *congruence* (**congruent, incongruent**), *time* (time point one to four) and *location*(hand, neck) was calculated.Significant interaction effects were analyzed with further ANOVAS.Pearson correlations were calculated between temperature and questionnaire scores for the significant effects.

## 3. RESULTS

### 3. 1 Questionnaire data

The 2 × 2 ANOVA (within subject factors *body* and*congruence*) revealed a significant main effect of *body* for the illusion questions, $F_{1, 20}$= 4.39, $P$ = .049, $\eta^2$ = .18, showing that in the body conditions the illusion questions were rated higher (*mean difference* = 1.87, *SE* = .70). In addition, the ANOVA also revealed an interaction ofbody and **congruence**,$F_{1, 20}$= 4.87, $P$ = .039, $\eta^2$ = .20. Bonferroni corrected post hoc t tests revealed a significant difference for the illusion score between **congruent** mannequin and object condition ($t_{20}$=2.58, $P$=.02), with the congruent mannequin condition being more illusory (*mean* = 9.83, *SD* = 5.16 versus *object**congruent** mean* = 7.29, *SD* = 5.48). There was no significant main effect of *congruence*(all $F$<.86,$P$ > .72).

The ANOVA for Q3, the feeling of having two bodies, revealed a significant main effect of *body* for the illusion questions, $F_{1, 20}$ = 6.42, $P$ = .02, $\eta^2$ = .24, showing that in the body conditions the feeling of having two bodies was rated higher (*mean difference* = 2.10, *SE* = .83). There were no other significant main effects or interactions (all $F$ <2.14, $P$ > .16).

The ANOVA for Q5, the perceived match between visual and vestibular signals, revealed a trend for the main effect of *congruence,* $F_{1, 20}$ = 4.19, $P$= .054, $\eta^2$ = .17,i.e. the **congruent**conditions were rated as more **congruent**(*mean difference* = 2.43, *SE* = 1.19). No other main or interaction effects were significant (all $F$<.70, $P$ > .41).

The ANOVA for Q6, the sickness measure, revealed no significantmain or interaction effects (all $F$ < 2.47, $P$> .13).

## 3.2 Temperature

### 3.2.1Skin temperature

In the repeated measures 2 × 2 × 4 × 2 ANOVA factors *body*,*congruence*, *time* and *location* there was a significant main effect of*congruence*, $F_{1, 18}$= 4.62, $P$ <.05, $\eta^2$ = .20, meaning that temperature in the **congruent** conditions decreased more than in the**incongruent** conditions. For the interaction effect of *body*× *congruence* × *time*× *location*Mauchly's test indicated a violation of the assumption of sphericity, $\chi^2_5$ = 20.96 , $P$ <.01. The degrees of freedom were therefore corrected using Huynh-Feldt estimates of sphericity($\varepsilon$ = .63) revealing a significant interaction effect of *body*×*congruence*×*time*× *location*, $F_{3, 16}$ = 3.70, $P$= .04, $\eta^2$ = .17. Moreover, there was a trend for the interaction of*congruence* × *time*, $F_{3, 16}$ = 2.80, $P$ = *.08*, after degrees of freedom were corrected using Huynh-Feldt estimates of sphericity ($\varepsilon$ = .59, Mauchly's test, $\chi^2_5$ = 20.96, $P$ <.01).No other main effect or interaction was significant ($F$<2.34, $P$ > .13).Since the four-way interaction effect was significant, we calculated two separate ANOVAs for each of the twoanatomical locations (hand, neck) to explore the data in more detail.

The 2 × 2 × 4 repeated measures ANOVA for the hands revealed a significant interaction effect of *body* ×*congruence* × *time*, $F_{3, 17}$ = 4.15, $P$= .04, $\eta^2$ = .18 (see Figure 4, left panel), after degrees of freedom were corrected using Huynh-Feldt estimates of sphericity ($\varepsilon$ = .51, Mauchly's test, $\chi^2_5$ = 32.70, $P$ <.01; all other $F$<2.16, $P$> .16).

Further ANOVAs for each time point for the hand revealed a significant main effect for *body* at time point one, $F_{1, 19}$ = 4.56,$P$= .04, $\eta^2$ = .19, (all other $F$ < 1.29, $P$ > .27). For time points2 and 3, no significant main or interaction effect emerged (all $F$ < 2.33, $P$ > .14). The ANOVA at time point 4showed an interaction effect of *body* ×

***congruence***, $F_{1,19} = 5.08$, $P = .04$, $\eta^2 = .21$ (see Figure 4, left panel). No main effect was significant (all $F < 1.77$, $P > .20$).

The 2 × 2 × 4 repeated measures ANOVA for the neck with factors *body*, *congruence* and *time* revealed only a trend for the main effect of*congruence* ($F_{1,18} = 4.25$, $P = .054$, $\eta 2 = .19$; all other F> 1.94,P >.16, see Figure 4, right panel).

**3.3 Correlations**

Pearson product-momentcorrelationswere calculated between the drop in temperature (mannequin **congruent** – mannequin **incongruent** at time point 4)and the illusion score as well as the scores toQ5 and Q3 (again **congruent – incongruent**).These analyses revealed no significant correlation (all $P > .12$).

**4. DISCUSSION**

The present study used a newly developedFBI setup to investigate how visuo-vestibular integration of bodily cues would modulate implicit and/or explicit illusory self-identification with another body(see reviews Blanke & Mohr, 2005; Lenggenhager *et al.*, 2006; Lopez *et al.*, 2008; Blanke, 2012; Pfeiffer *et al.*, 2014). These were the two main findings:

First, the *implicit*measure proved sensitive to our manipulation, that is, we found a drop in skin temperature specifically during the illusion condition. This is in line with our hypothesis based on studies that manipulated visuo-tactile**congruency** in a similar context(Petkova & Ehrsson, 2008; Salomon *et al.*, 2013). We thus argue that current models of body ownership (e.g. Petkova *et al.*, 2011), which typically include visual, tactile and proprioceptive modalities only, would gain from including the vestibular system, especially if such a model addresses full body ownership (compare also Lenggenhager & Lopez, in press; Lopez, 2013; Pfeiffer *et al.*, 2014).

Second, in contrast to our hypothesis and to studiesusing conflicts between other sensorymodalities, these implicit changeswere notentirely reflected by explicit measures; the illusion scores were generally rather low and while the illusion was stronger in the **congruent** mannequin condition than in the **congruent** object condition, there was no difference between**thecongruent** and the **incongruent** stimulation in the mannequin condition.

**4.1 Visuo-vestibular congruency induces a body-specific drop in temperature**

The temperature drop in the **congruent** mannequin condition indicates for the first time that a visuo-*vestibular* conflict might change the bodily self in predictable ways. Thermoregulation has been convincingly linked to altered ownership during similar full body and body part illusions through a modulation of the homeostatic activity (Moseley *et al.*, 2008; Kammers *et al.*, 2011; Salomon *et al.*, 2013). Thermoregulation is prominently mediated by the insula (e.g. Diwadkar *et al.*, 2013), which generally plays a role in interoceptive signaling (Craig, 2002, 2009; Critchley *et al.*, 2004). Interestingly, tight neuroanatomical and functional links between vestibular and interoceptivesystems based on shared representation in the insula have been demonstrated (see Balaban, 1999 for a review), making an influence of the vestibular system on thermoregulation plausible.

Our temperature data showed a main effect of congruency, i.e. a stronger temperature decreaseduringvisuo-vestibular **congruence**than**incongruence**. Motion sickness, elicited byvisuo-vestibular conflicts, hasbeenlinked to an altered thermoregulation (e.g. Hesse, 1874; Graybiel, 1969). However, the direction of temperature change is not conclusive (Holmes *et al.*, 2002; Nobel *et al.*, 2006, 2012; Ngampramuan *et al.*, 2014). Yet, motion sickness is unlikely to explain the temperature drop in our data as it did not differ between conditions, nor correlate with temperature alterations.Furthermore, the additionally significant interaction effectshows thatthe temperature drop wasbody-specific (i.e. stronger in the mannequin condition). This suggests thatthe temperature drop is not a pure interaction of multisensory conflict and thermoregulation, but importantly mediated by higher-level aspects of the bodily self, i.e.when the multisensorystimulationwascoherent and alsoplausiblefrom a top down perspective(seeing the body from a first personperspective)(compare Tsakiris & Haggard, 2005; Gallace *et al.*, 2014).

Remarkably we found this interaction effect for the hands, but not for the neck. Previous studies only measured skin temperature at anatomical locationsthat were visible during the experiment(Moseley *et al.*, 2008; Salomon *et al.*, 2013). Here, we used a thermocouple positioned at the neck of the participant, while the mannequin's neck was not seen (compare Figure 1A and B). This might suggest that the thermoregulation was only affected for body parts, which were actually seen during the multisensory stimulation.Such hypothesis is in line with limb-specific modulation of skin temperature during vision of (Sadibolova & Longo, 2014) or attention to (Patrizi, 1912)certain body parts. Alternatively, hand-neck differences could be related to the physiological response pattern of body temperature regulation: body temperature drops first in the periphery to conserve the temperature of life-supporting central organs.

Generally, the size of the effects were comparable to the findings of a recent visuotactile FBI (Salomon *et al.*, 2013), but much smaller than in the RHI (Moseley *et al.*, 2008).This difference might either be linked to methodological issues (e.g. stimulation time, measuring device, sampling rate), to different functional and cortical mechanisms of full body as compared to body part representations (see Blanke, 2012 for an overview) or to the novel combination of modalities manipulated in the present experiment (i.e. visuo-vestibular versus visuo-tactile integration in the previous experiments).

### 4.2 Visuo-vestibular congruence marginally influences phenomenological aspects of the illusion

Questionnaire data revealed a higher illusion score in the *mannequin **congruent*** as compared to the *object**congruent*** conditions, suggesting that self-identification with a mannequin is generally easier than with an object, most plausibly as a consequence of so-called top-down constraints (cp. Tsakiris & Haggard, 2005).

However, in contrast to comparable FBIs using **congruence** between other modalities (e.g.Petkova & Ehrsson, 2008), the illusion scores were rather low, and the congruency between visual and vestibular signal did not show the typical pattern of a stronger illusion in the **congruent** as compared to the **incongruent** condition. We suggest variousplausible mechanisms underlying this “negative” result.

Visuo-vestibular **congruence**might beharder to be consciously detectedthan visuo-tactile **congruence**. While it is rarely explicitly assessed in classical RHI or FBI (compare also discussion inSuzuki *et al.*, 2013), we can assume that participants areperfectly able to judge if a tactile and a visual event arepresented **congruently** or not, at least in the range of the delays used in those studies. This was less evident for the visuo-vestibular congruencyin our experimental setup, as shown by the mere trend for higher scoresin the **congruent** as compared to the **incongruent**conditions in the“congruence question” (Q5). We suggest that the difficulty in judgingcongruence might be caused by a strong tendency to integrate visual and vestibular signals into one single percept.Studies on the perception of self-motiondemonstrated that visual and vestibular inputs are generally integrated in a statistically optimal fashion, even when they are manipulated to generate conflicting signals. In these situations both,an overweighing of vestibular cues (Fetsch *et al.*, 2009; Butler *et al.*, 2011), as well a bias towards visual cues(Berger *et al.*, 2010; Prsa *et al.*, 2012), have been observed.Moreover, Ni and colleagues (2013) observed that gaze straight ahead dominates body straight ahead in determining the reference frame to define the perceived direction of motion, thus demonstrating that preference for vision-related variables extends also to the definition of space with respect to the self. The tendency to overweigh visual inputfits with our participants'high **congruence** judgment, independent of the condition. Moreover,there seems to be an inability to weigh visuo-vestibular signals uncoupled, causing a mandatory fusion of visual and vestibular input (Prsa *et al.*, 2012).This appears plausible as there is no distinct, conscious vestibular sense or percept (Angelaki & Cullen, 2008), and unlike other sensory stimulation, pure vestibular stimulation and sensation is very rare. In a nutshell, the vestibular system is intrinsically multisensory(Angelaki *et al.*, 2009).This corroborates the lack of a spatially confinedunimodal vestibular cortex (Guldin & Grüsser, 1998) and withthe fact thatcortical vestibular centers are highly multimodal(e.g. Büttner & Henn, 1976; Meng & Angelaki, 2010; for specific reviews see Blanke, 2012; Prsa *et al.*, 2012).

Yet, even if the **congruence**was not consciously detected, it is still unclear, why it did only influence implicit but not explicit measures.Recent studies using cardio-visual conflictshowed an explicit effect on body ownership both for the full body (Aspell *et al.*, 2013) as well as for the rubber hand (Suzuki *et al.*, 2013), even without the conscious differentiation of **congruence**and **incongruence**.Although implicit and explicit measurement were recorded at two different time points, we can rule out that the difference of temporal recording explains the lack of an effect or correlation between the two measuresas previous studies had to deal with the same temporal issue, but managed to show a connection between the skin temperature and the questionnaire data (Moseley *et al.*, 2008; Salomon *et al.*, 2013).

Another reason why we did not find a modulation of congruence on the questionnaire data might be related to the fact that the illusion-related ratings were generally rather low. This could potentially be linked to methodological problems (i.e. the perspective on the body) or the choice of questions used to assess the illusion (note that the two typical referral-of-touch questions fromBotvinick& Cohen(1998)were not adapted here). Alternatively and more interestingly, it could also be linked to the idea of stronger anchoring of the self through vestibular stimulation (Ferrè *et al.*, 2014). The vestibular system - similar to interoceptivesignaling (see Tsakiris *et al.*, 2011) - plays an important role in *anchoring* the self to the body (e.g.Bonnier, 1905; Blanke *et al.*, 2002, 2004; Blanke, 2004, 2012; Blanke & Mohr, 2005). It could thus be proposed that the additional veridical vestibular stimulation during our experimental conditions has increased the anchoring of the self to the body and thus decreased the FBI. Further experiments will be necessary to test this hypothesis.

### 4. 3 Limitations and Outlook

The visuo-vestibular **congruence** was barelydetected consciously by the participants in our experimental setup. Next to the strong tendency of the brain to integrate visuo-vestibular signals described above, this may have resulted from the fact that we have only used translational interauralaccelerations, as well as fromthe fact that the vestibular and the visual stimulation were only phase-shifted and spatially mirrored, but were along the same axis.Future studies might consider using different kinds of vestibular stimulations, which possibly elicit a stronger conflict between the visual and the vestibular modalities, yet it is important to avoid severe motion sickness. A variation of stimulation duration could furthercontrol for effects of adaptation to the visuo-vestibular conflict.Adding three-dimensional images to the seen video might make the seen motion more realistic, even more as recent finding that optimal visuo-vestibular cue integration is highly dependent on stereoscopic visual input (Butler *et al.*, 2011). The skin temperature drop as physiological correlate of ownership has recently been doubted on the grounds of a lack of replication of the data (Rohde *et al.*, 2013). These authors have shown that decreases in ownership are not always accompanied by corresponding decreases in skin temperature andargue that the temperature drop might ratherreflect changes in arousal or social contact during the tactile stimulation in the RHI(e.g. Moseley *et al.*, 2008). Additionally, they showed a dissociation between the cooling of the hand and the subjectively reported ownership over the hand, which fits nicely also to our findings.Thereby, we believe that our experiment might contribute to the discussion started by Rohde et al. (2013): While we cannot completely rule out the effect of arousal, using vestibular input delivered by a motion platform, we show that social contact is notmandatory to induce the cooling effect,corroborated by Salomon et al., (2013) who used a robot for tactile stimulation.Those inconsistencies but also similarities encourage further research to understand the cause of cooling in bodily illusionsbetter.

## 4.4 CONCLUSION

Results of the present experiment suggest that vestibular mechanisms importantly influence multisensory integration underlying the bodily self even if we might not be consciously aware of it.

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## ABBREVIATIONS

Full Body Illusion – FBI

Head mounted display – HMD

Rubber Hand Illusion - RHI

Standard error of mean – SEM

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## TABLES

Table 1.Questions shown after the four conditions presented in a randomized order. Gray shading indicates the questions that formed the "illusion score".

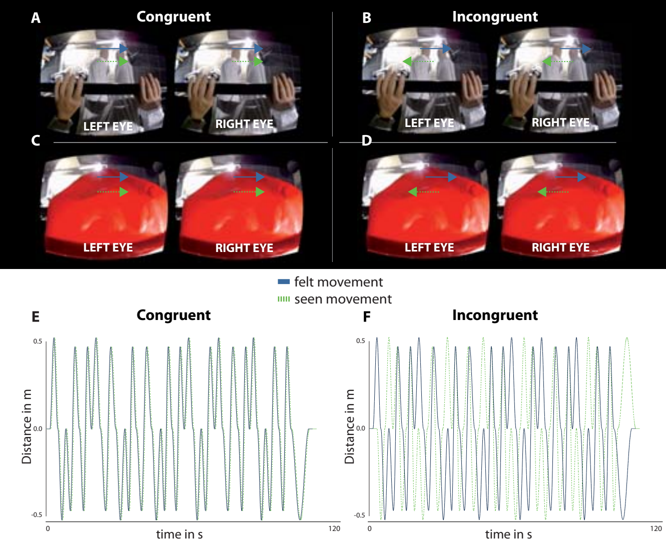
## FIGURES

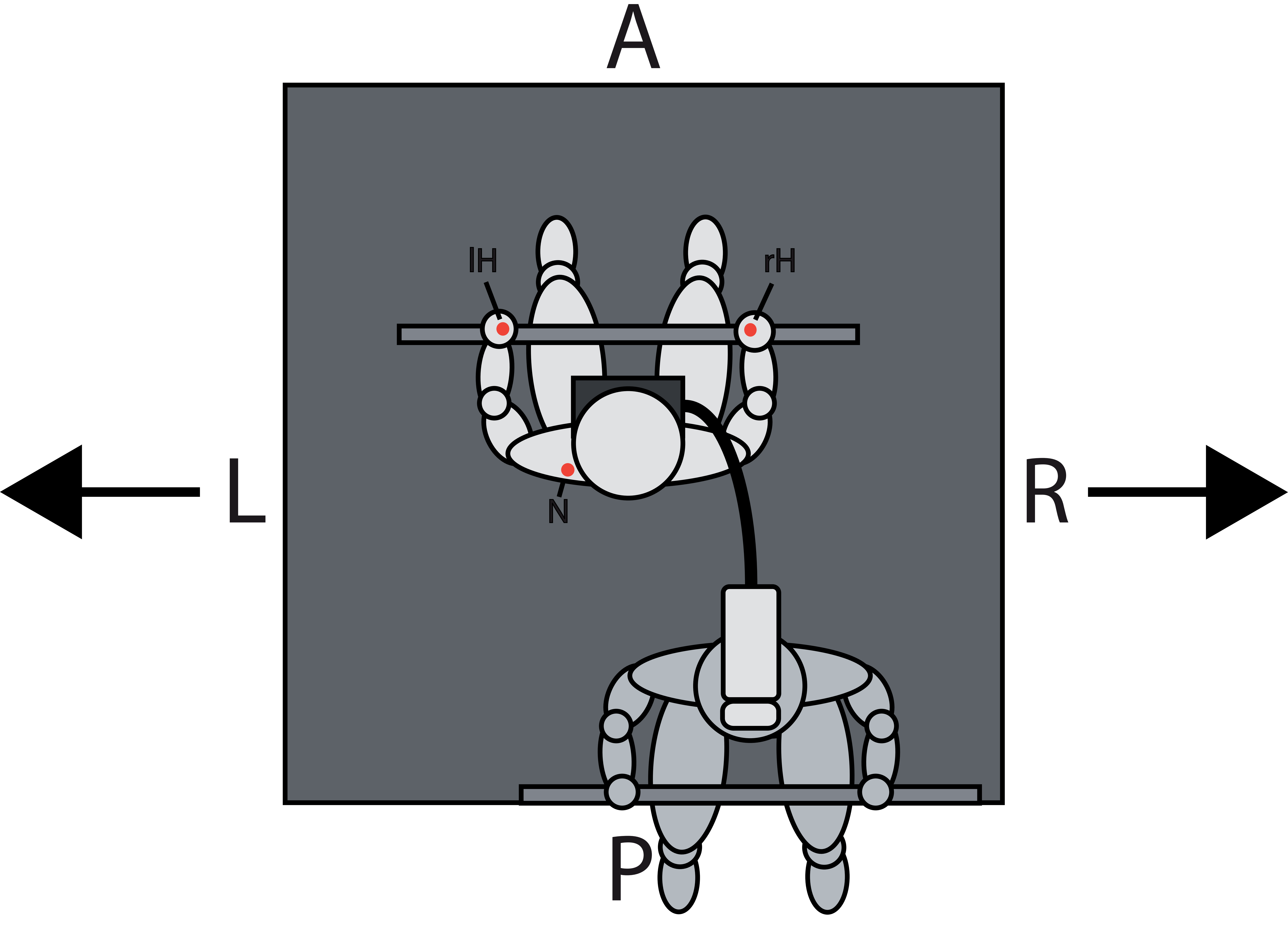
Figure 1.Experimental setup. Overall, the blue arrows and lines indicate the passive movement on the motion platform, which is sensed by the vestibular system while the green arrows and lines represent the seen movement of either the body (A and B) or the object (i.e. a red pillow) (C and D). A – D represent screenshots of the different conditions. E and F represent felt (blue) and seen (green) motion pattern.

Figure 2.Scheme of the experimental set-up from an aerial view. The participant was seated in the middle of the motion platform (dark grey) and faced to the anterior part (A), wearing an HMD connected to a webcam and having attached three thermo-couples (red dots, lH = left Hand, rH = right Hand, N = Neck). On the posterior part (P) of the platform a mannequin was positioned with a webcam above filming the movement. The motion platform was accelerated sinusoidally to the left (L) and to the right (R).

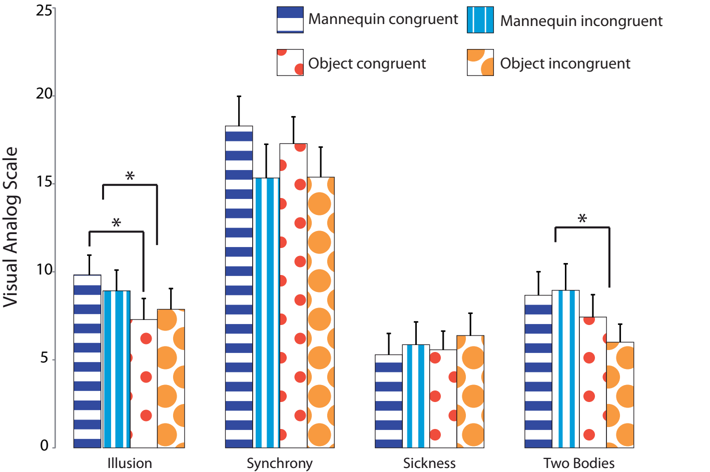
Figure 3. Questionnaire data. On the left, the averaged illusion scores on a visual analog scale (0 = disagree completely, 30 = agree completely) with the significant main effect of body (* = $p< 0.05$). In the middle, the values for the **congruence** judgment over all condition, with a trend for the main effect of delay.On the right the values for the sickness in each condition. Black lines show the standard error of the mean (SEM).

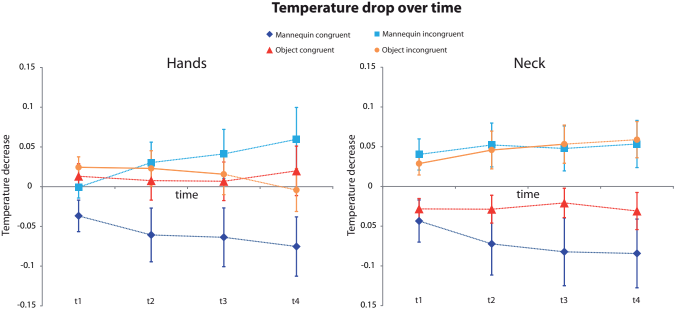
Figure 4. Changes of skin temperature in degree Celsius for the hands (left) and the neck (right) over time. Depicted are the four means for each condition (four different colors) and the SEM.


A
Congruent
B
Incongruent
LEFT EYE
RIGHT EYE
C
D
felt movement
seen movement
E
Congruent
F
Incongruent
Distance in m
0.5
0.0
-0.5
0
120
time in s


A
lH
rH
L
R
N
P

# Questionnaire Data




Temperature drop over time
Mannequin congruent
Mannequin incongruent
Object congruent
Object incongruent
Hands
Neck
Temperature decrease
time
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
t1
t2
t3
t4

# Supplementary Online Material

## Methods

*Room temperature*

In order to control for possible confounding effects of a change in room temperature over the different conditions, we first calculated a 2 × 2 × 4 repeated measures ANOVA with factors *body* (mannequin, object), *congruence* (congruent, incongruent), and *time* (time 1 to 4).

## Results

*Room temperature*

The repeated measures ANOVA for the room temperature revealed a significant main effect of time, $F_{3, 17}$= 24.32, $P < .01$, $\eta^2 = .56$, after degrees of freedom were corrected using Huynh-Feldt estimates of sphericity ( $\varepsilon = .43$, Mauchly's test, $\chi^2_5 = 50.94$, $P < .01$). Importantly, no other significant main or interaction effect was found, i.e. room temperature did not a priori differ between conditions.